

*TEPHRODYTES BRASSICARVALIS*, NEW GENUS AND SPECIES  
(ANURA: PELODYTIDAE), FROM THE ARIKAREEAN CABBAGE  
PATCH BEDS OF MONTANA, USA, AND  
PELODYTID-PELOBATID RELATIONSHIPS

AMY C. HENRICI

Scientific Preparator, Section of Vertebrate Paleontology

ABSTRACT

*Tephrodytes brassicarvalis*, n. gen. and sp., is based on the remains of a nearly complete skeleton, several partial skeletons, and some isolated bones from the Arikareean Cabbage Patch beds of western Montana, USA. It possesses the hallmark pelodytid character of a fused tibiale and fibulare and differs from other known pelodytids in the following unique combination of characters: 1) frontoparietal fontanelle concealed, 2) posterior tip of frontoparietal present, 3) otic plate of squamosal present, 4) otic ramus of squamosal reduced, 5) vertebral neural arches elongate, 6) sacral diapophyses widely expanded, and 7) anterior lamina of scapula absent.

Because the new anuran shares similarities with both pelodytids and pelobatids, and because the pelodytids have been included in the Pelobatidae, a cladistic analysis was undertaken to examine pelodytid-pelobatid relationships. This analysis also examines pelobatoid relationships. Results of this study reveal the following hypotheses of relationships. The Pelobatidae and Pelodytidae are best considered as separate families. *Miopelodytes*, *Pelodytes*, and *Tephrodytes*, whose relationships are unresolved, are members of the Pelodytidae. Similarities between *Tephrodytes* and some of the pelobatids are the result of convergence. Within the Pelobatinae *Eopelobates*, *Macropelobates*, and *Pelobates* form one clade, in which *Eopelobates* and *Pelobates* are sister taxa, and *Scaphiopus* and *Spea* form another. The *Eopelobatinae* is synonymous with the *Pelobatinae*. *Leptobrachium*, chosen as a representative taxon for the Megophryinae, is the sister taxon to the Pelobatinae.

INTRODUCTION

The Cabbage Patch beds, exposed in the Blackfoot, Flint Creek, Deer Lodge, and Divide intermontane basins of western Montana (Fig. 1), have yielded a diverse fauna that includes mammals, birds, reptiles, amphibians, and fish (Rasmussen, 1989). This study reports a new anuran genus and species, *Tephrodytes brassicarvalis*, in the family Pelodytidae, from these beds. The new taxon is based on a nearly complete skeleton, two partial skeletons, and isolated bones, all of which are well-preserved. They were collected by Donald Rasmussen from localities that he discovered in the Flint Creek Basin in Granite and Powell counties. These specimens and isolated bones are referred to a single species because comparison of them with the holotype, and each other, reveals no significant differences in their morphology. Other taxa of frogs also have been collected by Rasmussen from the Cabbage Patch beds, and these are under study by the author.

The Cabbage Patch beds are Arikareean, late Oligocene-early Miocene in age. During the Arikareean in western Montana a large basin, the Clark Fork Basin, was being filled predominantly with fluvial and lacustrine fine-grained, tuffaceous sediments (Rasmussen, 1989). Rasmussen (1977) suggested that the ash component in these sediments blew in from the west, possibly originating in the Cascades or the Columbia Plateau area, and was deposited in the uplands. From

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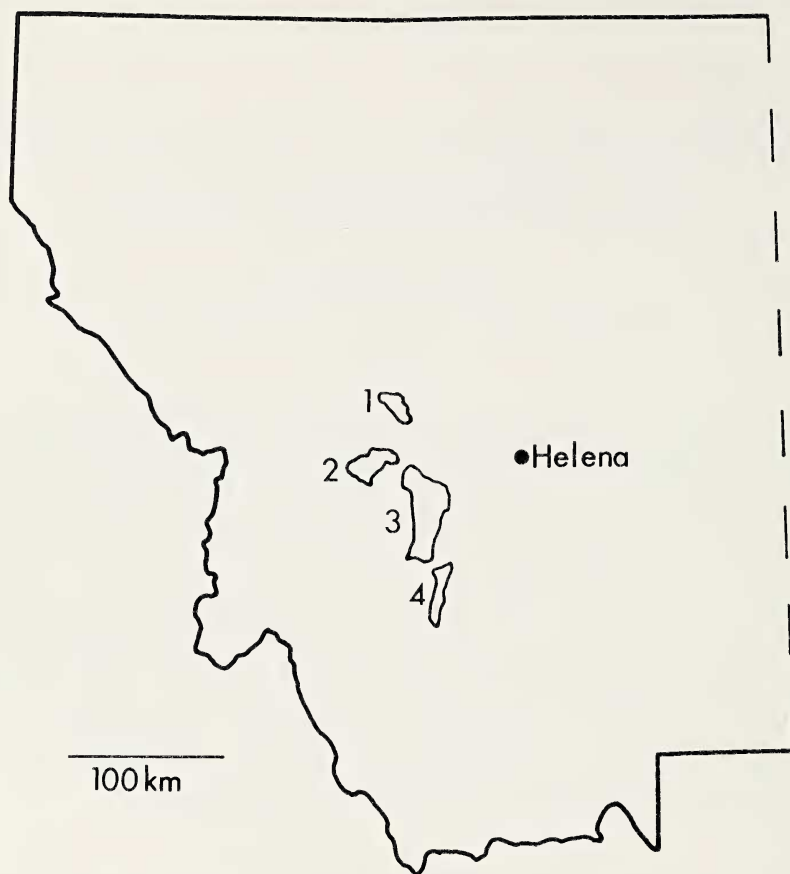


Fig. 1.—Map of western Montana showing the location of basins in which the Cabbage Patch beds are exposed (modified from Fields et al., 1985). The basin names are: 1) Blackfoot, 2) Flint Creek, 3) Deer Lodge, and 4) Divide. The pelodytid fossils came from the Flint Creek Basin.

there, Rasmussen (1977) further speculated, the ash was washed into the depositional basins, of which the Clark Fork was one, and was extensively reworked before final deposition. Only remnants of this formerly widespread unit exist today in the Flint Creek and adjacent basins (Rasmussen, 1989). The depositional environments of the three localities the fossils came from were determined to be fluvial overbank for localities KU-MT-12 and KU-MT-25, and lacustrine for locality KU-MT-8 (Rasmussen, 1977). The holotype came from KU-MT-25.

The Pelodytidae was named by Bonaparte in 1850 (Frost, 1985), although Cope (1866) is often given credit for naming the family. Boulenger (1897) included the pelodytids in the Pelobatidae, and since then the pelodytids have been ranked either as a separate family (Taylor, 1941; Lynch, 1973; Duellman, 1975; Sanchiz, 1978; Laurent, 1979; Dubois, 1983; Frost, 1985; Cannatella, 1985; Duellman and Trueb, 1986) or incorporated with the Pelobatidae (Noble, 1924, 1931; Griffiths, 1963; Kluge and Farris, 1969; Vergnaud-Grazzini, 1970; Špinar, 1972; Savage, 1973). More recent classifications consider the pelodytids a separate family (Lynch, 1973; Duellman, 1975; Laurent, 1979; Dubois, 1983; Frost, 1985; Cannatella,

1985; Duellman and Trueb, 1986; Ford and Cannatella, 1993). Because *Tephrodytes* possesses several features (sculpturing on the dermal skull bones, presence of posterior tip of the frontoparietal, frontoparietals cover frontoparietal fontanelle, squamosal articulates with maxilla, and presence of elongate vertebral neural arches) that also occur in some pelobatids, but were previously unreported for the pelodytids, an examination of the pelodytid–pelobatid relationship is warranted. Thus a cladistic analysis was undertaken to see if the new information from *Tephrodytes* helps to resolve whether the pelodytids should be placed in the Pelobatidae or in their own family. This analysis also addresses pelobatoid relationships which were unresolved in the cladistic analysis of anurans undertaken by Ford and Cannatella (1993).

The holarctic family Pelodytidae is not very diverse. Two extant species of *Pelodytes*, *P. punctatus* and *P. caucasicus*, occur in southwestern Europe and the Caucasus region of southeastern Asia, respectively (Frost, 1985). The occurrence of *Pelodytes* in the middle Pleistocene of France was recorded by Rage (1969) and he questionably referred some of the fossils to *P. punctatus* (Rage, 1972). *Pelodytes arevacus* and specimens attributed to *Pelodytes* are known from the middle Miocene of Spain (Sanchiz, 1978). *Miopelodytes* was the only pelodytid previously known from North America, and it is based on a single specimen from the middle Miocene Elko shales near Elko, Nevada (Taylor, 1941). Additional material, including tadpoles, has been collected from this locality and are being described by Dr. Ted Cavender (personal communication). *Propelodytes wagneri*, from the middle Eocene of Messel, Germany, was considered to be a pelodytid by Weitzel (1938). However, both Hecht (1963) and Sanchiz (1978) cast doubt on this assignment, and Wuttke (1988) has referred to these specimens as *Eopelobates wagneri*.

According to the most recent classification that includes fossil taxa (Duellman and Trueb, 1986) the family Pelobatidae includes 13 genera in three subfamilies. Seven of these are in the Megophryinae, which has no fossil record, and they occur in southeastern Asia and from the Indo-Australian Archipelago to the Philippine Islands (Duellman and Trueb, 1986).

The Eopelobatinae (Špinar, 1972) originally included only *Eopelobates*, which has a holarctic distribution and ranges from the early Eocene to the Pliocene. Nessov (1981) later added *Aralobatrachus* and *Kizylkuma*, which are based on isolated elements from the late Cretaceous of Uzbekistan, but these taxa have since been reassigned to the Discoglossidae (Roček and Nessov, 1993). Studies of the development of the frontoparietal by Roček (1981, 1988) have revealed that the frontoparietal in *Eopelobates bayeri* consists of three ossifications instead of two. The presence of the median ossification has been inferred for *E. anthracinus*, the genotype, and this character is included in the revised diagnosis for the genus (Špinar and Roček, 1984). Because the frontoparietal is apparently paired in the North American *Eopelobates grandis* and *E. guthriei*, Roček (1981) suggested that they are probably more closely related to *Scaphiopus* than to *Eopelobates*. I agree with his suggestion concerning *E. guthriei*. However, *E. grandis* possesses several features that do not support a close relationship with *Scaphiopus*. Both specimens are currently under study by the author. Kuhn (1941) described seven genera containing eight species that Estes (1970) later synonymized as *Eopelobates hinschei*. However, Roček (1981) questioned the taxonomic placement of these taxa, in part because the frontoparietal is apparently paired. Hereafter, discussion concerning *Eopelobates* will be limited to the well-described *E. anthracinus* and *E. bayeri*.

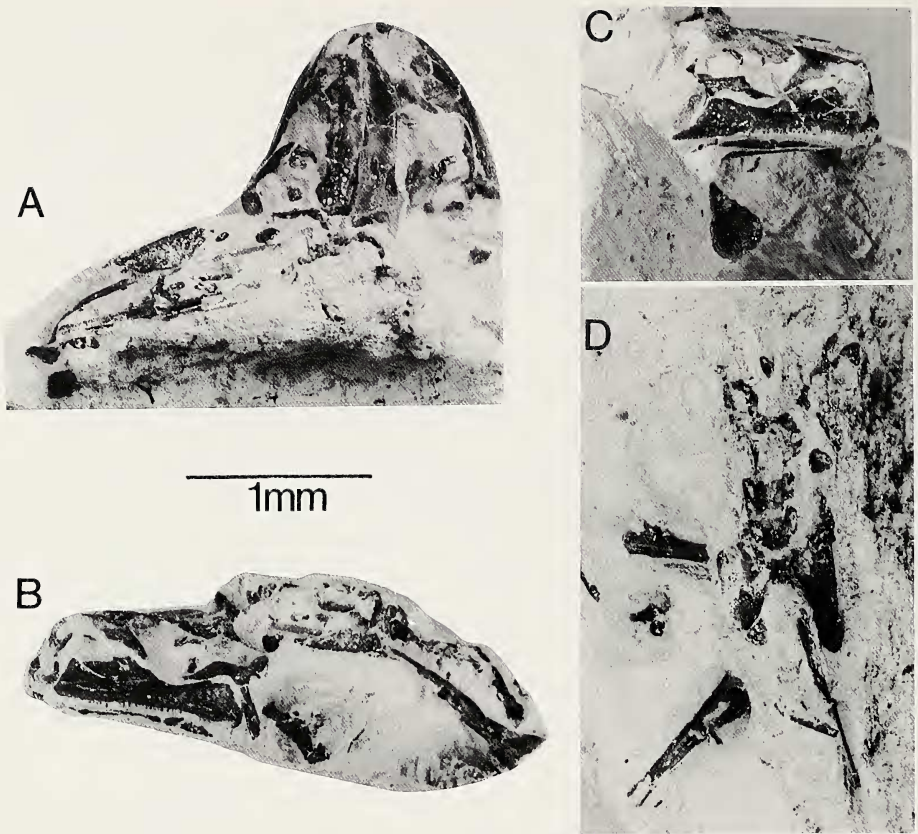


Fig. 2.—Photographs of the holotype of *Tephrodytes brassicarvalis*, KU 19928. A, dorsal view; B, left lateral view; C, right lateral view; and D, counterpart.

The fossorial Pelobatinae consists of the middle Oligocene *Macropelobates* from Mongolia, the extant *Pelobates* from Europe, western Asia, and North Africa, and the extant *Scaphiopus* from southern Canada to southern Mexico. The earliest record for *Pelobates* is the late Eocene of Belgium (Böhme et al., 1982) and that for *Scaphiopus* is the middle Oligocene of North America (Estes, 1970). If *E. guthriei* is indeed a species of *Scaphiopus*, then the record can be extended back to the early Eocene.

#### ABBREVIATIONS

*Anatomical.*—Al, anterior lamina of scapula; As, angulosplenic; At, anterior tubercle of scapula; C, columella; Cl, clavicle; D, dentary; Ex, exoccipital–prootic complex; F, femur; Fp, frontoparietal; H, humerus; Il, ilium; Is, ischium; M, metatarsals; Mx, maxilla; N, nasal; Op, otic plate of squamosal; Or, otic ramus of squamosal; Pal, palatine process of maxilla; Pm, premaxilla; Po, postorbital process of frontoparietal; Pp, posterior process of maxilla; Qj, quadratojugal; R, radio-ulna; S, sacrum; Sc, scapula; Sp, sphenethmoid; Sq, squamosal; Tf, tibiofibula; tTF, fused tibiale and fibulare; U, urostyle; V, vertebra; Zp, zygomatic process of maxilla.

*Institutional.*—AMNH, American Museum of Natural History; CM, Carnegie Museum of Natural History; FMNH, Field Museum of Natural History; KU, University of Kansas, Museum of Natural History; UNSM, University of Nebraska State Museum; and USNM, United States National Museum.

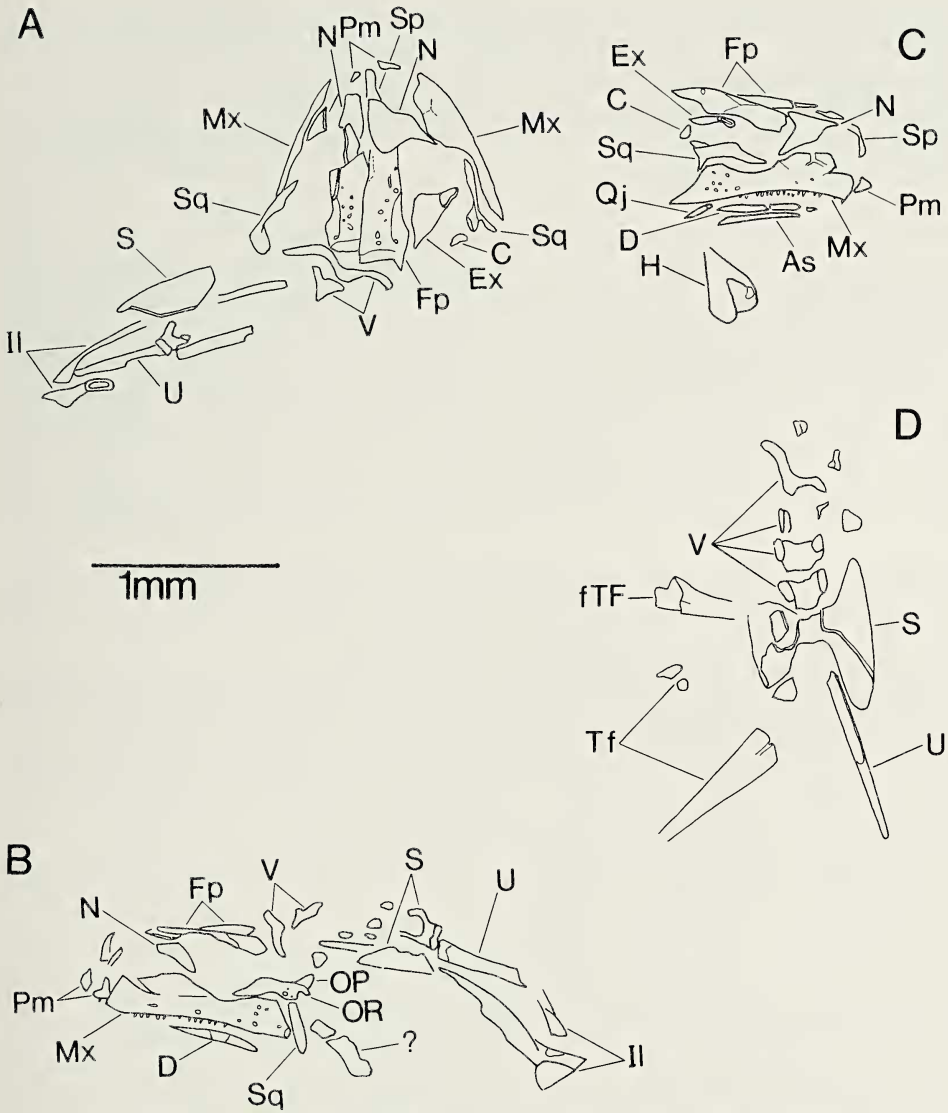


Fig. 3.—*Tephrodytes brassicarvalis*, KU 19928. Line drawings of same views as in Fig. 2.

SYSTEMATIC PALEONTOLOGY

Class Amphibia

Order Anura

Family Pelodytidae

*Tephrodytes*, new genus

*Type Species.*—*Tephrodytes brassicarvalis*, new species.

*Diagnosis.*—*Tephrodytes* differs from all other pelodytids by having frontoparietals that meet medially to conceal the frontoparietal fontanelle. It differs from *Pelodytes* in the following unique combination of characters that are not known for *Miopelodytes*: 1) posterior tip of frontoparietal present, 2) otic plate of squa-

mosal present, 3) presacral vertebral neural arches elongate, and 4) anterior lamina of scapula absent. It is distinguished from *Miopelodytes* by possession of reduced otic ramus of squamosal and expanded sacral diapophyses.

*Etymology.*—From the Greek *tephra*, ashes, and *dytes*, diver, enterer; in reference to the tuffaceous sediments from which this frog was recovered, and in which it may have estivated.

#### *Tephrodytes brassicarvalis*, new species

*Holotype.*—KU 19928 (Fig. 2, 3): partially complete, loosely articulated skeleton. The skull includes both frontoparietals, nasals, premaxillae, maxillae, squamosals, right ?quadratojugal, right exoccipital–prootic complex, right ?columella, right pterygoid, and both dentaries and angulosplenials. The postcranial skeleton is preserved in part and counterpart and includes: fourth through eighth vertebrae, sacral vertebra, urostyle, right humerus, right radio-ulna, both ilia, right tibiofibula, and right fused tibialae and fibularae.

*Type Locality and Horizon.*—KU-MT-25, Cabbage Patch #10; Flint Creek Basin, Powell County, Montana. Lower Cabbage Patch beds, Arikareean.

*Referred Specimens.*—From the type locality: KU 19221, partial left frontoparietal, left exoccipital–prootic complex, and vertebral column; KU 23489, right scapula and clavicle, sacral vertebra, urostyle, ilia, and hindlimbs; KU 18191, right maxilla; KU 19940, left maxilla; KU 18195, right ilium; KU 19917, left ilium; KU 19918, right ilium; KU 19919, right ilium.

From locality KU-MT-12, Cabbage Patch #4, Flint Creek Basin, Granite County, Montana, Middle Cabbage Patch beds, Arikareean: KU 18266, proximal half of right humerus; KU 18270, proximal end of fused tibialae and fibularae; KU 18273, proximal end of fused tibialae and fibularae.

From locality KU-MT-8, Pikes Peak #1, Flint Creek Basin, Powell County, Montana, Upper Cabbage Patch beds, Arikareean: KU 20654, sacrum; KU 20659, complete right humerus and proximal end of left humerus from different individuals.

*Diagnosis.*—As for genus (currently monotypic).

*Etymology.*—From the Latin *brassica*, cabbage, and *arvalis*, of a cultivated field, in reference to the Cabbage Patch beds.

#### *Description*

The holotype (Fig. 2, 3) is a three-dimensionally preserved, nearly complete skeleton in which the cranial bones are very closely associated. Its length, from tip of snout to distal end of urostyle, is approximately 4.0 cm. That this specimen had achieved adulthood before death is suggested by the well-ossified bones of the skull and postcranial skeleton. Measurements of complete bones appear in Table 1. The following description is based on the holotype unless otherwise stated.

*Skull.*—Both halves of the subrectangular frontoparietals are preserved in KU 19928 (Fig. 2A, 3A). The right half is slightly crushed along a small portion of the medial edge and its anteriormost end is covered by the right nasal. In the left frontoparietal the anterior half of the lateral edge is broken away, the postero-medial end lies underneath the posterior end of the right frontoparietal, and the posterior tip is covered by matrix and the left transverse process of the third vertebra.

The frontoparietal is widest near the posterior end (Fig. 2A, 3A, 4A). From the posterior end it narrows to the midpoint of its length where it flares slightly in a lateral direction to form the postorbital process (Fig. 4A). From there to the

Table 1.—Measurements for all complete bones of *Tephrodytes brassicarvalis*. The holotype is KU 19928.

	KU 18191	KU 19221	KU 19917	KU 19918	KU 19928	KU 20654	KU 20659	KU 23489
Frontoparietal length					7.3			
Frontoparietal width					2.0			
Nasal length					3.1			
Nasal width					4.5			
Maxilla length	12.5				10.4			
8th vertebra length		2.4			1.9			
Sacral diapophyses length					7.8	9.9		5.0
Sacral diapophyses width					6.8	8.0		
Urostyle length					11.2			
Scapula length								3.5
Humerus length							9.7	
Ilium length			20.7	17.5	18.3			14.0
Femur length								13.1
Tibiofibula length								13.9
Tibiale-fibulare length								6.8

anterior end the frontoparietal is slightly narrower (Fig. 3A). The medial edge of the left frontoparietal, where exposed, is straight. In Fig. 2 and 3, however, crushing along the medial edge of the right frontoparietal causes it to appear as though it is tapering. The posterolateral corner of the frontoparietal is drawn out to a point, the posterior tip (=processus paroccipitalis of Roček, 1981), which is oriented posteriorly. I prefer to use Estes' (1970) term posterior tip instead of the processus paroccipitalis of Roček (1981) to avoid confusing this process with the paroccipital process of the occiput.

Light sculpturing in the form of pits and grooves occurs on the relatively flat dorsal surfaces of the frontoparietals. The sculpturing is most pronounced on the posterolateral corner and is absent along the medial edge. In KU 19221 (Fig. 4A), a larger individual than the holotype, the posterior half of one frontoparietal is preserved. Sculpturing covers most of its dorsal surface, and the pits and grooves are larger.

Unlike other pelodytids the frontoparietal fontanelle was not exposed in *Tephrodytes*. In some anurans that have an exposed fontanelle, such as *Spea*, the frontoparietals are sutured together only at the posterior end. From there anteriorly the two halves are free, which allows exposure of the fontanelle. In *Pelodytes*, which also has an exposed frontoparietal fontanelle, even the posterior ends of the frontoparietals are not in contact. Concerning *Tephrodytes* the preserved portion of frontoparietal in KU 19221 has several small indentations along the medial edge which are interpreted here as a zigzagging suture scar (Fig. 4A). This provides evidence that the posterior halves of the frontoparietals were sutured together. In the holotype the medial edge of the right frontoparietal does not taper, indicating that the two halves would have been in contact, thus covering the fontanelle.

Nasal bones are preserved only in the holotype. The right is undistorted (Fig. 2A, 3A) but the left is incomplete and its posteromedial corner is covered by the anterior end of the left frontoparietal. The area where the two nasals meet medially

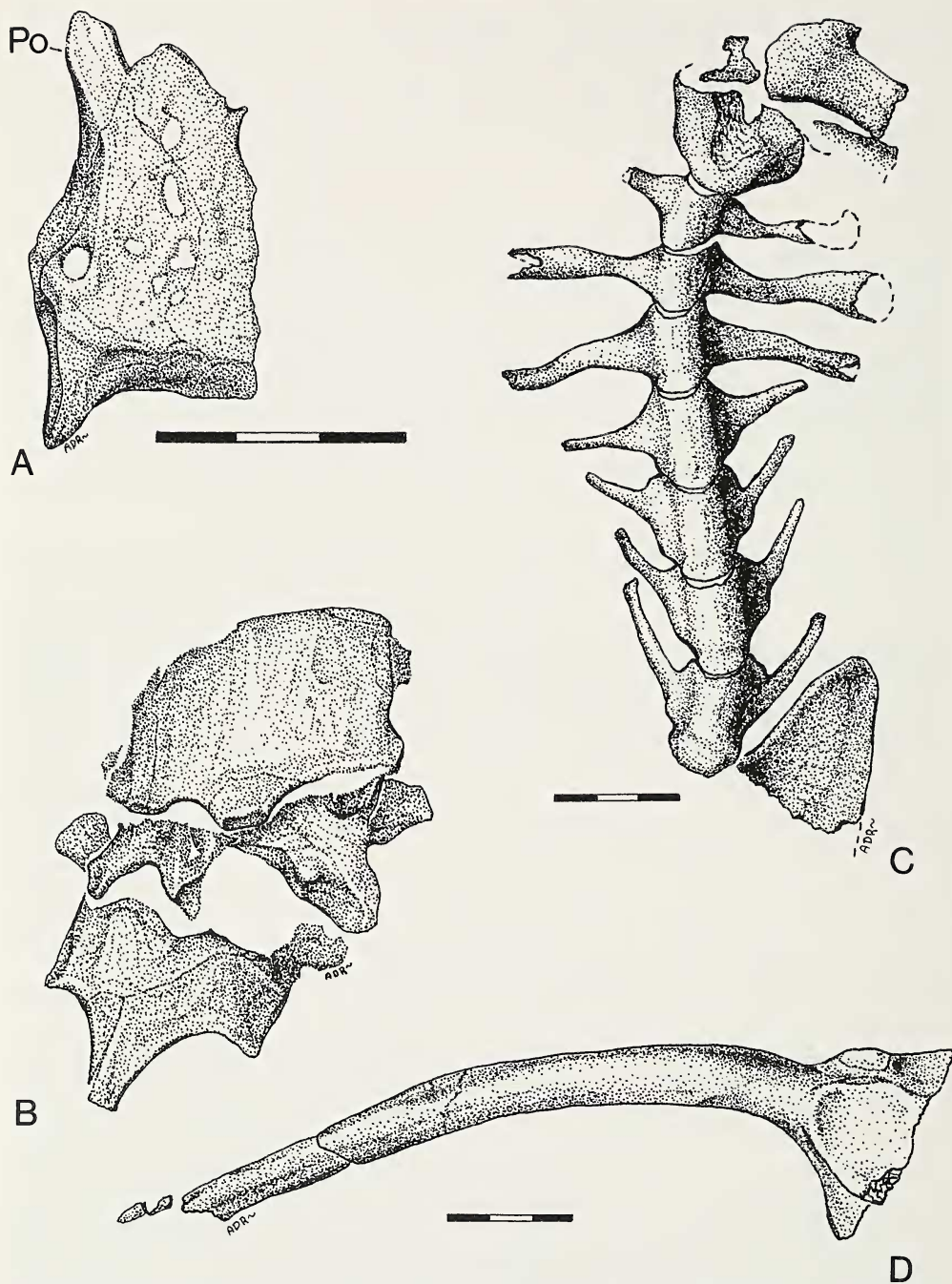


Fig. 4.—*Tephrodytes brassicarvalis*. A, posterior half of frontoparietal, KU 19921; B, presacrals 1–3, KU 19921; C, vertebral column and part of sacral diapophysis, KU 19921; and D, right ilium, KU 19917. Scale in mm, in which A and B are drawn to same scale.



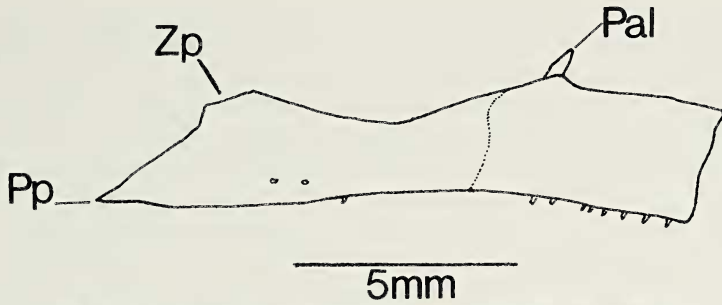


Fig. 5.—Right maxilla of *Tephrodytes brassicarvalis*, KU 18191.

is relatively long. The width of the right nasal is greater than its length (Table 1). Its anterior process is a small nubbin, and the concave anterolateral margin forms the posteromedial border of the external narial opening. Laterally, the nasal is drawn into a maxillary process which is directed posterolaterally (Fig. 2C, 3C). There is no sculpturing on the dorsal surface of the nasals.

The right and left premaxillae, which bear teeth, are preserved in the holotype (Fig. 2B, C; 3B, C). Here, the lateral ends of both premaxillae are overlain by the medial ends of the maxillae. The medial end of the left premaxilla is covered by the medial end of the right premaxilla. This telescoping causes the snout to appear narrower than it actually is. The alary process is elongate in the left premaxilla and incomplete in the right. Sculpturing is light and occurs as tiny pits but does not extend onto the alary process.

Both maxillae are preserved in the holotype (Fig. 2A, B, C; 3A, B, C). Two isolated maxillae (KU 18191, Fig. 5; and KU 19940) have also been recovered. In the holotype the pars facialis of the maxilla is slightly crushed at the anterior end where it reaches its greatest height. The pars facialis pinches in at the level of the orbit and increases in height at the posterior end to form the zygomatic process. In KU 18191 the dorsal surface of the zygomatic process is exposed and bears a suture scar, which provides evidence that the zygomatic ramus of the squamosal articulated with it. The posteroventral end of the maxilla is drawn into a point, the posterior process, which extends posteriorly beyond the level of the zygomatic process. Small teeth are present on the pars dentalis for about  $\frac{3}{4}$  the length of the bone from its anterior end. In the holotype the tip of a tooth that was prepared appears to be fang-like and recurved medially. In medial aspect, in KU 19940, the palatine process arises off the medial face of the pars facialis just dorsal to the pars palatina. In this specimen the tip of the palatine process is broken off at the level of the dorsal edge of the pars facialis. In KU 18191, exposed in lateral view, the tip of the palatine process extends beyond the dorsal edge of the pars facialis. It seems likely that the palatine process was long enough to reach, and articulate with, the lateral wing of the sphenethmoid, as in other pelobatoids. Sculpturing in the holotype is light and occurs as pits and grooves which are larger at the posterior ends of the maxillae. In KU 19940, the largest maxilla, only a few pits are present on the posterior end.

In the holotype there is a sliver of bone located adjacent to the posteroventral edge of the right maxilla. Based on its position and size it is believed to be the quadratojugal. Even if this bone is not the quadratojugal its presence in *Tephrod-*

*ytes* is suggested by the presence of a posterior process of the maxilla. Estes (1970) has implied that anurans possessing a posterior process also have a quadratojugal. To test Estes' theory I examined the skull of all anuran taxa in the CM amphibian osteology collection. With the exception of *Scaphiopus* and *Spea* all possessed a quadratojugal and the maxilla bore a well-developed posterior process. *Scaphiopus* and *Spea* were the only taxa that lacked a quadratojugal, and the posterior process of the maxilla was reduced or absent in these taxa.

Both squamosals are preserved in the holotype. The left squamosal is complete (Fig. 2A, B; 3A, B) and the right is missing the otic plate (Fig. 2A, C; 3A, C). The squamosals are pushed anteriorly out of position so that the ventral ramus of each is adjacent to the posterior end of the maxilla, causing the skull to appear shorter than it actually is. The zygomatic ramus of the squamosal is relatively thin and long, reaching its greatest thickness near the midpoint of its length. The otic ramus, in lateral aspect, is reduced to a nubbin. Projecting medially from the otic ramus is the otic plate which would overlap the crista parotica of the exoccipital-prootic complex, if the bones of the skull were articulated. The medial end of the otic plate is rounded. Sculpturing, consisting of a few large pits and some tiny pits, is mostly confined to the area where the three rami meet. A few small pits occur on the zygomatic ramus as well.

Only the right exoccipital-prootic complex is preserved in the holotype (Fig. 2A, 3A). Its medial end is pushed under the right frontoparietal and the lateral end is missing. There is a left exoccipital-prootic complex in KU 19221 in which the left frontoparietal covers its dorsal surface and the left parasphenoid alae covers its ventral surface. In this specimen the medial wall of the auditory capsule is exposed revealing the anterior and posterior acoustic foramina and the superior and inferior perilymphatic foramina. The presence of a dorsal endolymphatic foramen cannot be determined because of damage in the area where it would occur. The prootic foramen is not completely surrounded by bone.

A small, T-shaped bone lies ventral to the right exoccipital-prootic complex and medial to the posterior end of the right squamosal in the holotype. Based on its shape and position it is believed to be the medial end of the right columella. Note that only the footplate of the columella is visible in Fig. 3A and C. A small bone was found ventral to the columella and has been removed. This element is domed shaped, with a smooth dorsal surface and a rough ventral surface. Possibly it is a calcified operculum. It is equally possible that it is merely a fragment of weathered bone. The occurrence of a calcified operculum in a fossil frog is not unprecedented, as Kluge (1966) documented the presence of one in the lower Miocene *Scaphiopus neuter*. Unfortunately, I have been unable to compare the operculum of *S. neuter* with the possible operculum of *Tephrodytes*.

Preparation of the palatal region is hindered by the presence of the humerus, radio-ulna, and several unidentified bones underneath the skull. The right pterygoid, exposed in ventral view, bears an elongate anterior ramus, the anterior end of which lies between the lower and upper jaws. Although the exact length of the anterior ramus cannot be determined, it is unquestionably greater than twice the length of the medial ramus. The short medial ramus has a blunt medial end. The triangular posterior ramus is the shortest of the three rami. A portion of the left vomer is exposed in the holotype. Although several tooth sockets of the vomer are visible, no other details can be discerned.

Both lower jaws have been pushed dorsally inside the mouth of *Tephrodytes*. Not much of either dentary could be exposed by preparation because the maxillary

teeth overlap them (Fig. 2B, C; 3B, C). Only part of the angulosplenic (Fig. 2C, 3C) could be prepared without causing damage to the rest of the skull. Neither bone exhibits any noteworthy features.

*Postcranial Skeleton.*—The vertebral column is preserved as part and counterpart in the holotype (Fig. 2D, 3D). Presacrals four through eight and the sacrum are exposed, but there is considerable damage. In KU 19921 the eight presacrals and part of the left sacral diapophysis are exposed in ventral view (Fig. 4C), the atlas and first three presacrals are exposed in dorsal view (Fig. 4B), and the bone is well-preserved in all. The following description is based on KU 19921.

The eight presacral vertebrae have imbricate neural arches, as indicated by the elongate neural spine of the third presacral, the only one completely preserved and exposed (Fig. 4B). That the vertebrae are procoelous is best demonstrated in the seventh and eighth presacral (Fig. 4C). The atlantal cotyles of the atlas are closely juxtaposed. The dorsal surface of the atlantal neural arch is smooth. Its posterior end is drawn out to form the neural spine, the posterior end of which is broken off. Transverse processes of the second through fourth vertebrae are elongate and directed laterally, except for the fourth which is directed slightly posteriorly. The transverse processes of the fifth through eighth vertebrae are thinner and shorter. Those of the fifth are directed laterally, the sixth moderately anteriorly, and the seventh and eighth strongly anteriorly. Free ribs are not preserved and are presumably absent.

The sacral vertebra is preserved in the holotype (Fig. 2D, 3D), KU 23489 (Fig. 6), and KU 20654 (isolated sacrum). The diapophyses are widely expanded and their length is greater than their width. In the holotype length was determined from the right diapophysis of the counterpart. The width was determined by doubling the distance from the lateral edge of the left diapophysis to the middle of the centrum. In the holotype the length of the sacral diapophyses is roughly equivalent to the length of the last four presacrals. The length of four presacrals was determined by measuring the length of the eighth presacral, which has been exposed in dorsal view by preparation, and multiplied by four. Variation in the shape of the sacral condyle occurs. It is monocondylar in KU 23489, forming a dorsoventrally compressed oval and distinctly bicondylar in KU 20654. In the holotype it is neither distinctly monocondylar nor bicondylar but instead forms a flattened oval that is slightly pinched in the middle.

The urostyle is preserved as part and counterpart in the holotype (Fig. 2A, D; 3A, D), and in KU 23489 (Fig. 6) the anterior half of the urostyle is exposed. In the holotype it is at least as long as the last five presacral vertebrae. Transverse processes on the urostyle are not apparent in either example.

A right scapula and clavicle, exposed in KU 23489 (Fig. 6, 7B), are the only preserved bones of the shoulder girdle. The short, stocky scapula bears both the pars acromialis and glenoidalis on the ventral end and they are narrowly separated at their distal ends. Arising from the anterior edge of the scapula near the pars acromialis is the anterior tubercle. An embayment lies between it and the pars acromialis. The anterior tubercle also occurs in *Pelodytes*, and in that taxon the clavicle reaches the ventral edge of the anterior tubercle, and thus overlaps the scapula anteriorly. Because the ventral end of the scapula of *Tephrodytes* is very similar in shape to that of *Pelodytes*, it is inferred that the scapula is anteriorly overlain by the clavicle in *Tephrodytes*. In *Tephrodytes* the bone along the anterior edge of the scapula is somewhat thick and rounded, and the margin is concave. Thus, there is no anterior lamina.

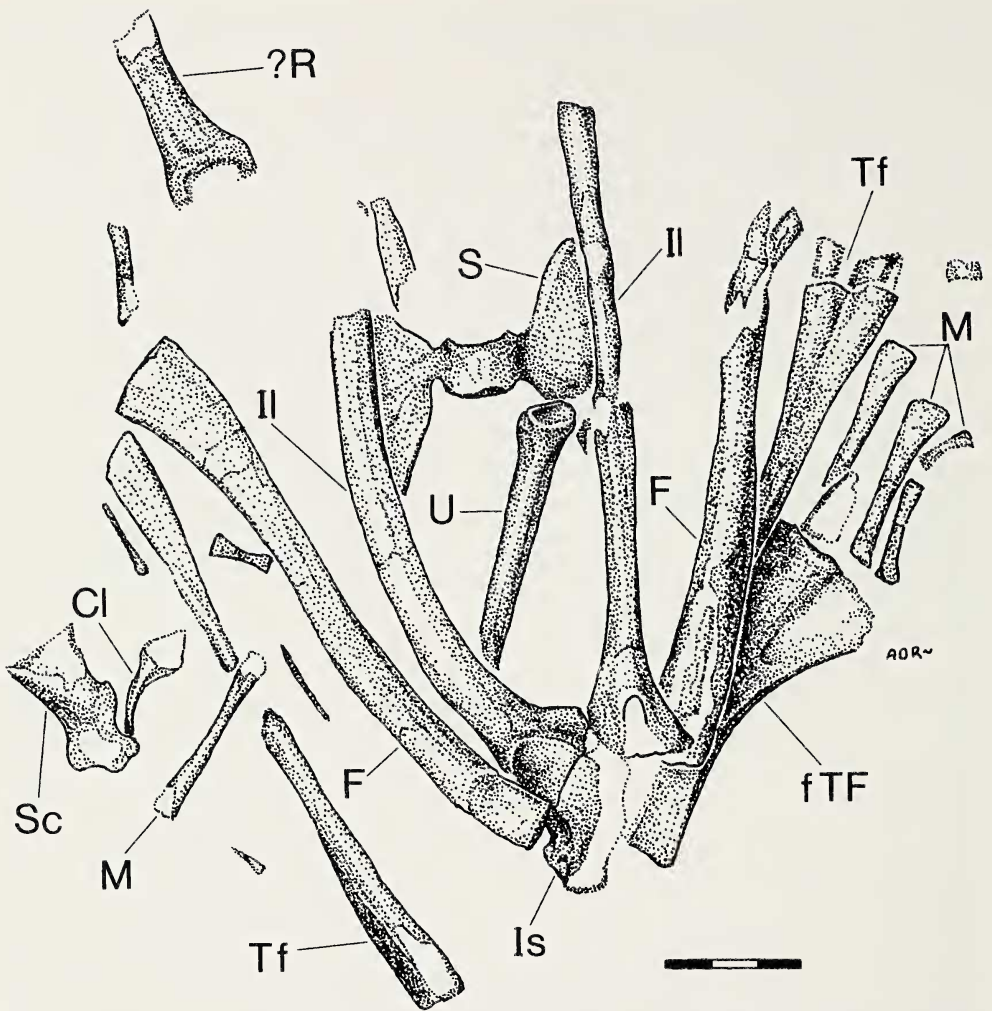


Fig. 6.—Postcranial skeleton of *Tephrodytes brassicarvalis* as preserved in KU 23489. Scale in mm.

The clavicle is oriented almost vertically in the matrix (Fig. 6). The process on the lateral end that articulates with the scapula is broken off and the medial end lies under the scapula. Enough of the clavicle is preserved to show that it is bowed, which suggests that the shoulder girdle of *Tephrodytes* is arciferal. The preserved portion of the clavicle is roughly the same length as that of the scapula. Thus, if the clavicle was complete it would be longer than the scapula.

The right humerus (Fig. 2C, 3C) and radio-ulna are preserved in the holotype in articulation. Here the humerus is exposed in dorsal and lateral views and the proximal third of this bone is missing. Also, there are three isolated humeri (KU 18266 and 20659, two humeri). The following description is based on KU 20659, a complete humerus. The shaft is straight and bears the crista ventralis on its proximal half. The triangular fossa is not very deep. Well-developed medial and lateral epicondyles bound the round humeral ball. The medial epicondyle pro-

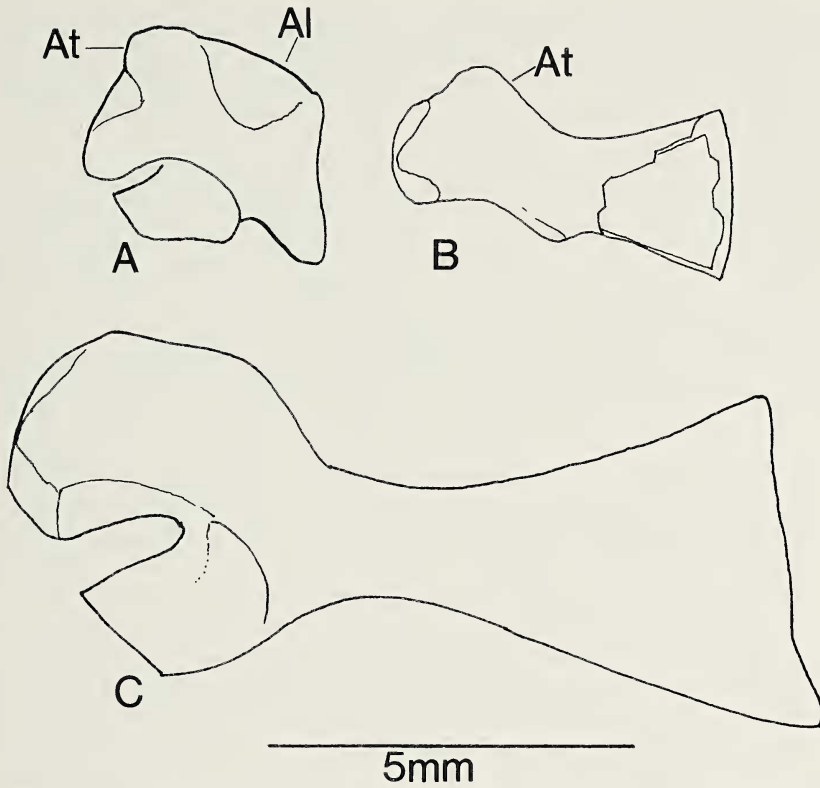


Fig. 7.—Comparison of scapula from specimens of similar size. A, *Pelodytes punctatus*, CM 54754; B, *Tephrodytes brassicarvalis*, KU 23489; C, *Scaphiopus holbrooki*, CM 92261.

trudes medially, is triangular in medial aspect, and is joined to the shaft by a thin crest. The smaller lateral epicondyle is crest-like. In lateral view a groove, the surface of which is covered with finished bone, lies between the roughened bone of the lateral epicondyle and the ball. The triangular olecranon scar is medially situated.

The radio-ulna is exposed in lateral view, and the anterior half of the bone is also exposed in dorsal view. The posterior end is poorly preserved, hindering its preparation. The olecranon process is rounded. A sulcus is not visible on the anterior half of the shaft. Also, in KU 23489 there is a bone that is possibly a radio-ulna (Fig. 6).

Both ilia are preserved in the holotype. The left is complete whereas the right is missing most of its shaft. There are several isolated ilia; the best preserved is KU 19917 (Fig. 4D). In that specimen, the shaft, which lacks crests, is bowed ventrally and has an oval cross section. The dorsal acetabular expansion bears an oval, dorsolaterally-projecting dorsal protuberance which has roughened, unfinished bone on its surface. This protuberance is larger in KU 19917 than in the holotype, which is a smaller individual. A groove runs from the shaft to the dorsal acetabular expansion. The ventral acetabular expansion and the dorsal acetabular expansion are subequal in length. The acetabulum is large, roughly bell-shaped, and somewhat deep. Its dorsal border projects slightly from the lateral surface of

the dorsal acetabular expansion whereas the ventral border projects strongly from the lateral surface of the ventral acetabular expansion. The dorsal ends of both ischia are preserved in KU 23489 (Fig. 6), in which they appear to be medially fused. The ischia do not extend greatly posteriorly as occurs in *Eopelobates* and *Megophrys* (Zweifel, 1956; Estes, 1970).

Both femora and tibiofibulae are preserved in KU 23489 (Fig. 6) and partial tibiofibulae occur in the holotype. The femur is slightly S-shaped, and the distal end is wider than the proximal end. Presence of a femoral crest cannot be determined because of the orientation of the femora in the matrix. In KU 23489 the tibiofibula is slightly longer than the femur (Table 1). The longitudinal sulcus of the tibiofibula is restricted to the proximal and distal ends.

Complete fusion of the tibiale and fibulare occurs in *Tephrodytes*. The left fused tibiale and fibulare is preserved in the holotype where it lies underneath the sacrum (Fig. 2D, 3D). In KU 23489 a left fused tibiale and fibulare is partly overlain by other bones (Fig. 6). Two isolated fused tibiale and fibulare (KU 18270 and 18273, Fig. 8) were recovered as well. In the former two examples the longitudinal sulcus is restricted to the proximal and distal ends. In the latter two examples, which are considerably smaller and missing their extreme distal ends, the longitudinal sulcus extends most of the length of the bone. The latter two bones are probably from juveniles. In all examples, the fused tibiale and fibulare have an hourglass shape and a small foramen is located near the midpoint of the shaft.

Only a few metatarsals and phalanges are preserved in KU 23489 and the holotype making it impossible to determine the phalangeal formula. Metatarsals 1-4 are preserved very close to the distal end of the left fused tibiale and fibulare (Fig. 6). A small phalanx is associated with metatarsal 1. None of the distal tarsal bones are preserved; possibly they were cartilaginous. A prehallux modified as a spade has not been found and presumably was absent, as in *Pelodytes*.

#### Family Assignment

*Tephrodytes brassicarvalis* possesses a fused tibiale and fibulare, which occurs only in the frog families Pelodytidae and Centrolenidae. Of the numerous characters that distinguish the pelodytids from the centrolenids (Duellman and Trueb, 1986) three are preserved in *Tephrodytes*, and are: the atlantal cotyles are closely juxtaposed, the vertebral neural arches are imbricate, and the sacral diapophyses are widely expanded. *Tephrodytes* possesses no characters that occur in the centrolenids but not in the pelodytids, thereby making its affinity with the pelodytids certain. Those characters that would indicate centrolenid affinities are: nonimbricate neural arches, dilated sacral diapophyses, and scapula not overlain anteriorly by clavicle.

During the course of this study I became aware of some inconsistencies in several of the characters used in different definitions of the Pelodytidae. Taylor (1941), Lynch (1973), and Duellman and Trueb (1986) all included in their definitions the fusion of presacral vertebrae I and II. None of the eight specimens of *Pelodytes punctatus* that I examined had fused presacral vertebrae. They were also free in the *P. punctatus* specimens examined by Cannatella (1985). Sanchiz (1978), however, observed the free state in *Pelodytes arevacus*, *P. caucasicus*, and both the free and fused states in *Pelodytes punctatus*. He concluded that in *P. punctatus* the free state occurred in both subadults and adults. Zweifel (1956), apparently following Taylor (1941), stated that they are fused in *Pelodytes*, although neither author mentioned which species were examined. In *Miopelodytes*

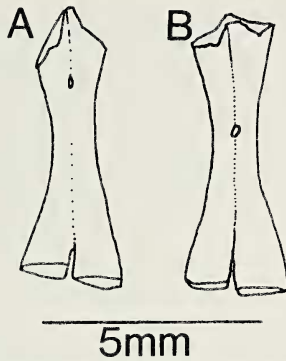


Fig. 8.—Fused tibiale and fibulare of *Tephrodytes brassicarvalis*. A, KU 18273; B, KU 18270.

Taylor observed that the first two presacrals are fused. However, I found this impossible to determine in *Miopelodytes* because of bone damage. Thus, fusion of presacrals I and II is not diagnostic of the family and appears to be variable in *Pelodytes*.

In his definition of the Pelodytidae, Lynch (1973) reported that the articulation between the sacrum and the urostyle is monocondylar, whereas in their definition of the family, Duellman and Trueb (1986) stated that it is bicondylar. Furthermore, Boulenger (1896), Taylor (1941), and Rage (1974) observed that the articulation is bicondylar, and Cannatella (1985) reported it as monocondylar. Zweifel (1956) suggested that the type of articulation varies intraspecifically. Sanchiz (1978) contested Zweifel's (1956) conclusion because he observed that the sacral condyle of *Pelodytes arevacus* and *P. punctatus* has a unique condition of being intermediate between the monocondylar and bicondylar states. In *Tephrodytes* the form of the sacral condyle varies, being either monocondylar, bicondylar, or the intermediate condition described by Sanchiz (1978). The type of articulation cannot be determined for *Miopelodytes*. Thus, it appears that the type of articulation between the sacrum and urostyle is a variable feature within the family.

Both Lynch (1973) and Duellman and Trueb (1986) included the presence of transverse processes of the urostyle in their definitions of the Pelodytidae. However, of the eight specimens of *Pelodytes punctatus* that I examined, only one possessed distinct transverse processes on the urostyle. In this specimen, CM 54318F, the process on the right side is well-developed whereas that of the left is a nubbin. The presence or absence of transverse processes does not appear to be the result of variation between the sexes because they were both present and absent in the females examined. Age as the cause of variation can be ruled out because the specimens examined were of similar size. Geographical variation also is not a factor because the specimens were from a single locality. Neither *Miopelodytes* nor *Tephrodytes* bears transverse processes on the urostyle. Thus, the presence of transverse processes of the urostyle varies in *P. punctatus*, has not been reported for either *Miopelodytes* or *Tephrodytes*, and should not be regarded as a diagnostic character of the family.

Evans and Milner (1993) noted that the ilia of *Pelobates* possess a spiral groove at the base of the shaft whereas pelodytids lack this groove. All of the pelodytid and pelobatid specimens that I examined possess this spiral groove, with the exception of *Miopelodytes*. The presence of a spiral groove could not be determined

in *Miopelodytes* because of damage to the ilium. Also, Sanchiz's (1978) illustrations of the ilium of *Pelodytes arevacus* and *P. punctatus* depict a groove. This character is possibly diagnostic of the Pelobatoidea, although I have not surveyed its distribution outside of the primitive anurans.

#### PELOBATOID RELATIONSHIPS

The monophyly of the Pelobatoidea has been established by Cannatella (1985), and confirmed by Ford and Cannatella (1993). Supporting synapomorphies for this hypothesis of relationship are the presence of an ossified sternum, the presence of a palatine process of the maxilla (Cannatella, 1985; Ford and Cannatella, 1993), and the presence of the adductor longus muscle (Cannatella, 1985). Cannatella (1985) deviated from traditional classifications that include the megophryines in the Pelobatidae by placing the megophryines in their own family, the Megophryidae. Following his taxonomy, the Pelobatoidea thus includes the Megophryidae, Pelobatidae, and Pelodytidae. He concluded, based on a cladistic analysis of primitive anurans, that the pelodytids and pelobatids are more closely related to each other than either is to the megophryids. Fossil taxa were not included in his study. However, Ford and Cannatella (1993), in a cladistic analysis of anurans, determined that the Megophryidae, Pelobatidae, and Pelodytidae form an unresolved trichotomy. The extinct Eopelobatinae were removed from the Pelobatidae by Ford and Cannatella (1993) because these workers questioned the monophyly and relationships of this group. Thus, they considered the Eopelobatinae to be a metataxon, having either uncertain relationships within the Pelobatoidea or comprising a sister group to the Pelobatoidea. This left *Pelobates*, *Scaphiopus*, and *Spea* as the remaining members of the Pelobatidae. The extinct pelobatine *Macropelobates* was not included in their study.

Previous studies have suggested somewhat different hypotheses of relationships. Lynch (1973) proposed that the pelodytids are the sister group of the pelobatids and higher anurans, whereas Sokol (1981) suggested that *Pelodytes* is most closely related to the megophryine and pelobatine pelobatids. Boulenger (1899) hypothesized that *Pelodytes* is more closely related to *Pelobates* than to *Scaphiopus*.

There has been considerable debate concerning the relationship of the extinct *Eopelobates* and *Macropelobates* to other pelobatids. Zweifel (1956) suggested that *Eopelobates* could be a subgenus of the megophryine genus, *Megophrys*. Similarly, Kluge (1966) considered *Eopelobates* to be more closely related to the megophryines than to the pelobatines. Estes (1970) observed that *Eopelobates* is a primitive member of the family that is similar to both the megophryines and the pelobatines. However, the above conclusions were based, in part, on examination of *E. grandis* and *E. guthriei*, which may not be species of *Eopelobates* (Roček, 1981). Derivation of the pelobatines and the megophryines from the eopelobatines was suggested by Špinar (1972). Roček (1981), on the other hand, observed that both *Eopelobates* and *Pelobates* possess a frontoparietal derived from three ossifications, a right and left ossification and a medial ossification situated posterior to them. He homologized the medial ossification with the extrascapular of *Eusthenopteron*. Because *Eopelobates* and *Pelobates* are the only anurans known to share this feature, Roček (1981) concluded that they evolved separately from all other anurans. This hypothesis was rejected on the basis of parsimony by both Cannatella (1985) and Milner (1988), and Milner has further suggested that the medial ossification is merely a synapomorphy defining a clade within the Pelobatidae.



A common ancestor, possibly *Macropelobates* (Noble, 1924), or a form close to *Macropelobates* (Zweifel, 1956; Estes, 1970) has been suggested for *Scaphiopus* and *Pelobates*, although Estes (1970) has cautioned that *Macropelobates* occurred too late in time to be the actual ancestor. Roček (1982) theorized that *Macropelobates* is more closely related to *Scaphiopus* than *Pelobates* based on morphological similarities and paleogeographical grounds. The Turgai Straits, which separated Europe and Asia from the Jurassic to the Eocene, would have prevented dispersal of pelobatines into Europe from an Asian ancestor (Roček, 1982).

### Cladistic Analysis

To obtain a better understanding of the interrelationship of the pelobatoids, a cladistic analysis was undertaken. Representative pelobatoids employed in the ensuing character analysis are as follows: *Leptobrachium*, *Eopelobates*, *Macropelobates*, *Pelobates*, *Scaphiopus*, *Spea*, *Miopelodytes*, *Pelodytes*, and *Tephrodytes*. A list of species examined is presented in Table 2. *Leptobrachium* was chosen as a representative megophryine because it is possibly the most primitive member of that group (Estes, 1970). Character states for *Eopelobates* were determined from the text, figures, and photographs in Estes (1970), Špinar (1972), and Špinar and Roček (1984). Only *E. anthracinus* and *E. bayeri* were considered because the status of other species in this genus has been questioned (Roček, 1981). For *Macropelobates* the character states were determined from examination of the holotype and an undescribed, disarticulated specimen, consisting mostly of postcranial bones, that was discovered in the collections of the American Museum of Natural History by Max K. Hecht. Because this specimen exhibits no differences from the holotype of *Macropelobates*, other than being slightly smaller, I concur with Hecht's identification of it. The descriptions of *Macropelobates* by Noble (1924), Estes (1970), and Roček (1981, 1982) were also used. For *Miopelodytes* character states were ascertained from examination of the holotype. Character states for the remaining anurans were determined through examination of dry skeletons and cleared and stained specimens. In this study *Spea* is treated as a genus, even though it is commonly considered to be a subgenus of *Scaphiopus*, to avoid problems in assigning character states for features in which the two taxa differ. For each character, polarity assessments were based on the outgroup algorithm (Maddison et al., 1984). *Alytes*, *Bombina*, and *Discoglossus* comprised the outgroup. The distribution of character states for the outgroup can be found in Table 3. Some of the characters used in the analysis are new, although the majority of them come from the studies of Zweifel (1956), Kluge (1966), Estes (1970), Špinar (1972), Sanchiz (1978), Roček (1981, 1982), Špinar and Roček (1984), and Cannatella (1985).

*Character Analysis.*—A total of 25 cranial and postcranial characters were analyzed in this study. These characters are discussed below.

1. Sculpturing commonly occurs on the outer surface of pelobatoid dermal skull bones. Although the style of sculpturing varies (i.e., pits and grooves, pustulose) and the distribution and amount of sculpturing on dermal skull bones varies, only its presence or absence is noted here. *Leptobrachium*, *Spea*, and *Pelodytes* lack sculpturing on dermal skull bones (state 0). Sculpturing (state 1) occurs in *Eopelobates*, *Macropelobates*, *Pelobates*, *Scaphiopus*, and *Tephrodytes*. Taylor (1941) made no mention of whether dermal skull bone sculpturing occurs in *Miopelodytes*. However, the squamosal, which was not identified by Taylor (1941) in his description of the holotype, bears sculpturing on the zygomatic and

Table 2.—List of Recent and fossil specimens examined.

Taxon	Skeleton	Cleared and stained
Recent		
Bombinatoridae		
<i>Bombina bombina</i>		2
<i>Bombina orientalis</i>		2
Discoglossidae		
<i>Alytes obstetricans</i>		2
<i>Discoglossus jeanneae</i>		2
<i>Discoglossus pictus</i>	1	
Pelobatidae		
<i>Leptobrachium hasselti</i>	1	
<i>Leptobrachium montanum</i>	1	
<i>Megophrys monticola</i>	1	1
<i>Pelobates cultripes</i> (adult)	2	2
<i>Pelobates cultripes</i> (tadpole series)		36
<i>Pelobates fuscus</i>		2
<i>Scaphiopus couchi</i>	3	2
<i>Scaphiopus holbrooki</i>	6	
<i>Scaphiopus hurteri</i>	1	
<i>Spea bombifrons</i>	5	2
<i>Spea hammondi</i>	2	
<i>Spea intermontanus</i>	1	
Pelodytidae		
<i>Pelodytes punctatus</i>	2	8
Fossil		
Pelobatidae		
<i>Macropelobates osborni</i>	2	
<i>Scaphiopus skinneri</i>	1	
Pelodytidae		
<i>Miopelodytes gilmorei</i>	1	

otic rami. Poor preservation and their orientation in the matrix prevents the identification of sculpturing on other dermal skull bones.

2. The frontoparietal of pelobatoids is either paired (state 0), consisting of a right and left half, or is tripartite (state 1), being composed of a right and left ossification and a medial ossification situated posterior to them (Roček, 1981, 1988). The frontoparietal is paired in *Leptobrachium*, *Scaphiopus*, *Spea*, *Miopelodytes*, *Pelodytes*, and *Tephrodytes*.

Roček (1981) has documented the tripartite condition in *Pelobates fuscus*, *P. syriacus*, and *Eopelobates bayeri*, and has inferred it for *E. anthracinus* (Špinar and Roček, 1984). I have observed it in cleared and stained tadpoles of *P. cultripes*. Roček (1981) noticed that during the ontogeny of the frontoparietal in *Pelobates* the three ossifications fuse together leaving no trace of a suture. In adults of *Eopelobates bayeri* the median suture is visible although it does not extend to the posterior end of the bone because of the medial ossification (Roček, 1981; Špinar and Roček, 1984).

For *Macropelobates* neither Noble (1924:fig. 1) nor Estes (1970:fig. 27) illustrated a median suture of the frontoparietal. However, Roček (1981) detected a

Table 3.—Distribution of character states among taxa used in the phylogenetic analysis. 0 indicates the primitive state, 1 and 2 derived states, and 9 missing or inapplicable data. Usage of 1 and 2 does not imply consecutively derived states.

	Character numbers																										
	1	2	3	4	5	6	7	8	9	1	1	1	1	1	1	1	1	2	2	2	2	2					
	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	
<i>Leptobrachium</i>	0	0	1	0	1	0	0	0	1	0	1	0	0	0	1	1	0	1	1	1	1	0	1	0	0	0	
<i>Eopelobates</i>	1	1	1	1	1	1	1	0	9	9	9	9	1	1	1	1	0	0	1	1	1	1	0	0	0	0	0
<i>Macropelobates</i>	1	0	1	1	9	9	1	9	9	9	9	1	0	1	1	0	0	9	1	9	1	0	9	1	0	0	
<i>Pelobates</i>	1	1	1	0	1	1	0	1	0	1	0	1	1	1	1	0	0	1	1	1	0	0	1	1	0	1	1
<i>Scaphiopus</i>	1	0	1	1	0	1	1	1	2	0	1	1	0	0	1	1	0	1	0	0	0	0	0	1	1	1	
<i>Spea</i>	0	0	0	1	0	0	0	1	2	0	1	1	0	0	1	1	0	1	0	0	0	0	0	1	1	1	
<i>Miopelodytes</i>	1	0	0	9	9	9	1	0	9	9	9	9	1	0	0	9	9	9	9	9	0	1	9	0	0	0	
<i>Pelodytes</i>	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	1	0	1	0	1	0	0
<i>Tephrodytes</i>	1	0	1	1	0	1	0	0	9	1	9	1	1	1	0	1	1	0	9	9	0	1	9	0	1	9	0
<i>Discoglossus</i>	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Alytes</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Bombina</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

small notch on the posterior margin of the frontoparietal in *Macropelobates* which is asymmetrical on the dorsal surface and symmetrical on the posterior surface. Because this notch divides the frontoparietal into two symmetrical halves, he suggested that it is paired. I found that in the holotype the median suture can be clearly observed at the posterior end of the frontoparietal, arising from the notch, thereby providing direct evidence for the paired nature of the frontoparietal in *Macropelobates*.

3. In some anurans the two halves of the frontoparietal do not meet along the midline of the skull, which allows exposure of the frontoparietal fontanelle (state 0). This occurs in *Spea*, *Miopelodytes*, and *Pelodytes*. The frontoparietal bones are in contact medially and thus cover the frontoparietal fontanelle (state 1) in *Leptobrachium*, *Eopelobates*, *Macropelobates*, *Pelobates*, *Scaphiopus*, and *Tephrodytes*.

4. The posterolateral corner of the frontoparietal of some pelobatoids is drawn out to a point, the posterior tip (state 1). This occurs in *Eopelobates*, *Macropelobates*, *Pelobates*, *Scaphiopus*, *Spea*, and *Tephrodytes*. *Leptobrachium* and *Pelodytes* lack the posterior tip of the frontoparietal (state 0). The condition in *Miopelodytes* cannot be determined.

5. The anterolateral margin of the nasal of pelobatoids varies in shape, being either concave (state 0), forming the posterior border of the narial opening, or straight (state 1). The margin is concave in *Pelobates*, *Scaphiopus*, *Spea*, and *Tephrodytes*. *Leptobrachium* and *Eopelobates* have a straight margin. Cannatella (1985) considered the anterolateral narial margin in *Pelodytes* to be straight. However, because the specimens that I examined all have a concave margin, I consider the state for *Pelodytes* to be primitive.

In a reconstruction of the skull of *Macropelobates*, Estes (1970) suggested that the anterolateral margin of the nasal is concave. However, this portion of the bone is not preserved (Noble, 1924; Roček, 1982), and thus the shape of the anterolateral margin is unknown. The condition of the nasal in *Miopelodytes* cannot be determined.

6. The zygomatic ramus of the squamosal either does not articulate with the maxilla (state 0), or articulates with the maxilla (state 1). In *Leptobrachium*, *Spea*,

and *Pelodytes* it does not articulate with the maxilla. The squamosal articulates with the maxilla in *Eopelobates*, *Pelobates*, *Scaphiopus*, and *Tephrodytes*. In *Macropelobates* the anterior end of the zygomatic ramus of the left squamosal and the posterior end of the left maxilla are both broken away, thereby eliminating direct evidence of their articulation, or lack thereof. Roček (1982) observed that the dorsal portion of the broken edge of the maxilla is very thick, indicating a strong zygomatic process (processus zygomaticomaxillaris of Roček, 1981), with which the zygomatic ramus of the squamosal articulates. However, the presence of the palatine process at the anterior end of the maxillary fragment indicates that the preserved portion of maxilla formed the ventral border of the orbit. Thus, the thickened bone Roček (1982) believed to be the zygomatic process is actually the orbital margin. Therefore, it cannot be determined if the squamosal articulated with the maxilla in *Macropelobates*. Although Taylor (1941) made no mention of it, a right squamosal, bearing both a zygomatic and otic ramus, is preserved in the holotype of *Miopelodytes*. Unfortunately, it cannot be determined if the zygomatic ramus of the squamosal articulated with the zygomatic process of the maxilla because the bones are not preserved in articulation and the portion of the maxilla where the zygomatic process would be, if present, is covered by a portion of the pterygoid.

7. The otic ramus of the squamosal in lateral view is either a tiny nubbin (state 0) or is slightly elongate and somewhat deep (state 1). The otic ramus is reduced in *Leptobrachium*, *Spea*, *Pelodytes*, and *Tephrodytes*. It is well-developed in *Eopelobates*, *Macropelobates*, *Pelobates*, *Scaphiopus*, and *Miopelodytes*.

8. The quadratojugal is present (state 0) in *Leptobrachium*, *Eopelobates*, *Pelobates*, *Pelodytes*, and *Tephrodytes*. It is absent (1) in *Scaphiopus* and *Spea*. In *Macropelobates* its presence or absence is controversial. Noble (1924) did not mention this bone in his description of *Macropelobates*. Estes (1970) argued for the probable presence of the quadratojugal, as he observed that the maxilla bore a posterior process with which the quadratojugal would articulate. Roček (1982) observed that the posterior end of the maxilla is broken away and that the bone along this break, in the posteroventral corner, is very thin suggesting that the posterior process was absent, and thus the quadratojugal was absent. However, the presence of the palatine process and teeth on the dentary process indicates that the preserved portion of maxilla is from the orbital region and not the posterior end of the maxilla, as suggested by Roček (1982). Because there is no solid evidence for the presence or absence of the quadratojugal, its state is here considered to be unknown. It cannot be determined if the quadratojugal was present in *Miopelodytes*.

9. The postchoanal ramus of the vomer, when present, forms the posterior border of the internal nares. A short postchoanal ramus (state 0) occurs in *Pelodytes*. This ramus is absent (state 1) in *Pelobates* and *Leptobrachium*. *Scaphiopus* and *Spea* possess an elongate postchoanal ramus (state 2) that almost reaches the maxilla. The presence or absence of the postchoanal ramus remains unknown in *Eopelobates*, *Macropelobates*, *Miopelodytes*, and *Tephrodytes* due to the incompleteness of these specimens.

10. In *Pelodytes* and *Tephrodytes* the anterior ramus of the pterygoid is elongate, being greater than twice the length of the medial ramus (state 1). The anterior ramus of the pterygoid is less than twice the length of the medial ramus (state 0) in *Leptobrachium*, *Eopelobates*, *Pelobates*, *Scaphiopus*, and *Spea*. The pterygoid

is incompletely known in *Macropelobates* and *Miopelodytes*. In *Eopelobates* the length of the rami has not been described.

11. The parahyoid bone is present (state 0) in *Pelodytes* and is absent (state 1) in *Leptobrachium*, *Pelobates*, *Scaphiopus*, and *Spea*. It has not been identified for *Eopelobates*, *Macropelobates*, *Miopelodytes*, and *Tephrodytes*. However, this character is considered to be unknown for these anurans because it is impossible to determine whether the parahyoid bone does not occur or was not preserved in these frogs.

12. The neural arch of the presacral vertebrae either barely extends beyond the level of the posterior zygapophyses (state 0) or forms an elongate spine which extends posteriorly beyond the level of the posterior zygapophyses (state 1). *Leptobrachium* and *Pelodytes* have vertebral neural arches that are not elongate. The vertebral neural arches are elongate in *Eopelobates*, *Macropelobates*, *Pelobates*, *Scaphiopus*, *Spea*, and *Tephrodytes*. Unfortunately, this character cannot be assessed in *Miopelodytes* because of damage.

13. The transverse processes of the last two presacral vertebrae of pelobatoids are directed either moderately anteriorly (state 0), or strongly anteriorly (state 1). Those directed moderately anteriorly are not situated close alongside the vertebral centrum and do not reach the level of the anterior zygapophyses of the preceding vertebra. In contrast, those directed strongly anteriorly tend to lie close alongside the vertebral centrum and the tips of the transverse processes almost reach the level of the anterior zygapophyses of the preceding vertebra. *Leptobrachium*, *Macropelobates*, *Scaphiopus*, and *Spea* possess transverse processes with a moderately anterior orientation. They are directed strongly anteriorly in *Eopelobates*, *Pelobates*, *Miopelodytes*, *Pelodytes*, and *Tephrodytes*.

14. In some pelobatoids the sacral diapophyses are expanded (state 0) whereas in others they are widely expanded (state 1). Traditionally, for descriptive and comparative purposes, the length of the sacral diapophyses has been compared to the equivalent number of vertebrae (Zweifel, 1956; Estes, 1970; Roček, 1982). For example, the length of the sacral diapophyses of *Scaphiopus* is equal to the length of two presacral vertebrae whereas those of *Pelobates* are equal to the length of four presacral vertebrae (Zweifel, 1956). This method works well with Recent specimens but is difficult to apply to fossils because the vertebral centra are commonly not exposed or poorly preserved. Instead, for the purpose of this study, sacral diapophyses considered to be expanded are those having a width greater than length. Widely expanded sacral diapophyses are those having a length greater than width. Expanded sacral diapophyses occur in *Leptobrachium*, *Scaphiopus*, *Spea*, and *Miopelodytes*, whereas widely expanded diapophyses occur in *Eopelobates*, *Macropelobates*, *Pelobates*, *Pelodytes*, and *Tephrodytes*.

15. In pelobatoids the scapula is either short (state 0) or long (state 1). The scapula is considered to be short if its length is less than that of the clavicle, and long if its length is greater than that of the clavicle. *Pelodytes* and *Tephrodytes* have a short scapula. It is long in *Leptobrachium*, *Eopelobates*, *Pelobates*, *Scaphiopus*, and *Spea*. In *Miopelodytes* the right scapula is preserved but neither clavicle is preserved. However, when the scapula of *Miopelodytes* is compared to the scapula from a *Scaphiopus* specimen of similar size, it is apparent that the scapula of *Miopelodytes* is short. For *Macropelobates* a similar comparison with *Pelobates* reveals that the scapula is long.

16. Some pelobatoid scapulae bear an anterior lamina (state 0), which is a thin

ridge of bone along the anterior edge of the scapula. An anterior lamina occurs in *Eopelobates*, *Macropelobates*, *Pelobates*, and *Pelodytes*. It is absent (state 1) in *Leptobrachium*, *Scaphiopus*, *Spea*, and *Tephrodytes* (Fig. 7). The presence or absence of the anterior lamina cannot be determined with certainty in *Miopelodytes*.

17. Both *Tephrodytes* and *Pelodytes* bear a small tubercle, the anterior tubercle, at the anterior margin of the ventral end of the scapula (state 1, Fig. 7). *Leptobrachium*, *Macropelobates*, *Pelobates*, *Scaphiopus*, and *Spea* lack the anterior tubercle (state 0). Spinar (1972) makes no mention of this tubercle in his detailed description of the scapula of *E. bayeri*, so it is most likely absent. Unfortunately, the presence or absence of the anterior tubercle cannot be determined for *Miopelodytes* because the scapular bone is so badly damaged.

18. The clavicle either overlaps the scapula anteriorly (state 0) or abuts the scapula's ventral edge, and thus does not overlap it anteriorly (state 1). In Recent pelobatids the scapula is not overlain anteriorly by the clavicle (Lynch, 1973; Trueb, 1973; Duellman, 1975; Duellman and Trueb, 1986). However, some confusion exists as to whether or not the scapula is anteriorly overlain by the clavicle in the pelodytids. Trueb (1973), and Duellman and Trueb (1986) stated that the scapula is not anteriorly overlain by the clavicle, whereas Lynch (1973) and Duellman (1975) pointed out that the scapula is partially overlain by the clavicle. Examination of specimens of *Pelodytes*, in which the clavicle and scapula are in articulation, shows that the scapula is anteriorly overlain by the clavicle. The scapula is anteriorly overlain by the clavicle in *Pelodytes* and *Tephrodytes*, and is not overlain in *Leptobrachium*, *Eopelobates*, *Pelobates*, *Scaphiopus*, and *Spea*. The state of this character cannot be determined in *Macropelobates* and *Miopelodytes*.

19. The medial end of the coracoid is considered to be expanded if the width of the medial end is greater than the width of the lateral end (state 1). It is expanded in *Leptobrachium*, *Eopelobates*, *Macropelobates*, and *Pelobates*. The medial end is not expanded (state 0) in *Scaphiopus*, *Spea*, and *Pelodytes*. The coracoids of *Miopelodytes* and *Tephrodytes* are not known.

20. The sternum is ossified (state 1) in *Leptobrachium*, *Eopelobates*, *Pelobates*, and *Pelodytes*. It is cartilaginous in *Scaphiopus* and *Spea* (state 0). A sternum has not been identified in *Macropelobates*, *Miopelodytes*, and *Tephrodytes*. Possibly an ossified sternum was present but not preserved in these taxa. Therefore the state of this character is considered to be unknown.

21. The ischium does not extend posteriorly beyond the dorsal acetabular expansion of the ilium (state 0) in *Pelobates*, *Scaphiopus*, *Spea*, *Miopelodytes*, *Pelodytes*, and *Tephrodytes*. It does extend posteriorly beyond the dorsal acetabular expansion of the ilium (state 1) in *Leptobrachium*, and *Eopelobates*. Both Zweifel (1956) and Estes (1970) illustrate the ischium of *Macropelobates* as not extending greatly posteriorly. My examination of this genus has convinced me that the ischium does extend greatly beyond the level of the dorsal acetabular expansion. The difference in our interpretations could be because the specimen has been extensively prepared in the time between their study and mine. Also, Estes (1970) reconstructed the pubis as unossified, although Noble (1924) pointed out that it was either ossified or that there was no room for it. This difference in interpretation caused Estes (1970) to orient the ischium somewhat incorrectly, making it appear as though it did not extend posteriorly.

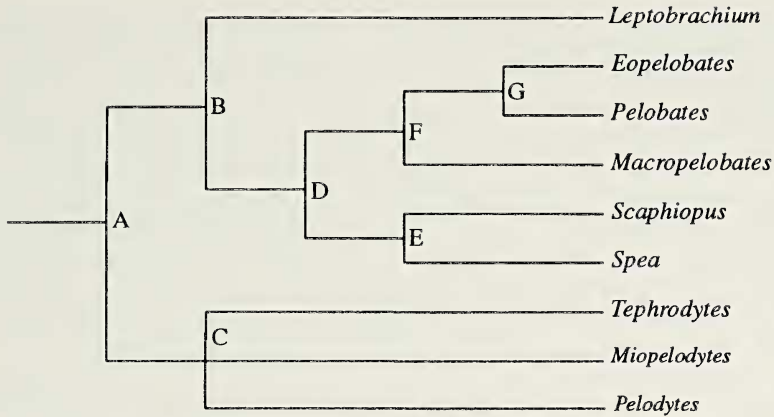


Fig. 9.—Consensus of two phylogenies for the Pelobatoidea. Synapomorphies supporting each node are discussed in the text.

22. Typically, the tibiale and fibulare of adult anurans are fused at their proximal and distal ends (state 0). However, those of *Miopelodytes*, *Pelodytes*, and *Tephrodytes* are completely fused to form a single bone (state 1).

23. Pelobatoids have either three free distal tarsal bones (state 0) in which distal tarsals 1 and 2 are free and distal tarsals 3 and 4 fused, or two free distal tarsal bones (state 1) in which distal tarsal 1 is free and distal tarsals 2, 3, and 4 are fused (Lynch, 1973). *Eopelobates* and *Pelodytes* possess three distal tarsal bones, whereas *Leptobrachium*, *Pelobates*, *Scaphiopus*, and *Spea* possess two. The number of distal tarsal bones is unknown for *Macropelobates*, *Miopelodytes*, and *Tephrodytes*.

24. In some pelobatoids the prehallux is modified as a bony spade which enhances burrowing ability. A spade is absent (state 0) in *Leptobrachium*, *Eopelobates*, *Pelodytes*, *Miopelodytes*, and *Tephrodytes*. It occurs (state 1) in *Macropelobates*, *Pelobates*, *Scaphiopus*, and *Spea*.

25. In *Scaphiopus* and *Spea* the gracilis muscle partially overlaps the sartorius muscle and its tendon, thereby partially concealing these structures (state 1). The gracilis muscle does not partially conceal the sartorius muscle and its tendon in the other extant pelobatoids (state 0). Obviously, the state for this character cannot be determined in the fossil taxa *Eopelobates*, *Macropelobates*, *Miopelodytes*, and *Tephrodytes*.

*Results.*—Two equally parsimonious trees were generated by PAUP (version 3.0S for Macintosh, Swofford, 1991) utilizing the branch and bound method in which the trees were rooted using the outgroup method. The trees have a length of 54 steps and the consistency index is 0.519. All characters were treated as unordered. Although PAUP was run using both the ACCTRAN and DELTRAN optimizations, the results presented here are based on the trees obtained using the ACCTRAN optimization because it favors reversals. A consensus of the two trees is presented in Fig. 9.

The results of this cladistic analysis differ from those of Cannatella (1985) and Ford and Cannatella (1993). Here, the monophyletic Pelobatoidea is divided into two, well-supported clades, the Pelodytidae and the Pelobatidae. *Tephrodytes* is

a member of the Pelodytidae, but its relationships with *Miopelodytes* and *Pelodytes* are unresolved. The Pelobatidae includes the representative megophryine *Leptobranchium*, *Eopelobates*, *Pelobates*, *Macropelobates*, *Scaphiopus*, and *Spea*. That *Eopelobates* is a member of the Pelobatidae is well-supported. However, because it is most closely related to *Pelobates*, it should be considered a member of the Pelobatinae, thereby making the Eopelobatinae a synonym of the Pelobatinae.

Autapomorphies for the Pelobatoidea were not included in this study because they do not contribute toward resolution of pelobatoid relationships. Thus, the synapomorphies of the Pelobatoidea in this study all exhibit homoplasy and are: anterior lamina of scapula absent (character 16, state 1), which reverses to present (state 0) at Node F and *Pelodytes*; and sternum ossified (character 20, state 1), which reverses to cartilaginous (state 0) in *Scaphiopus* and *Spea*.

The Pelodytidae is united at Node C by three nonhomoplasious characters and one that exhibits homoplasy. These are: anterior ramus of pterygoid elongate (character 10, state 1); scapula with anterior tubercle (character 17, state 1); posterior presacral vertebrae with transverse processes oriented strongly anteriorly (character 13, state 1), which also evolves at Node F; and tibiale and fibulare completely fused (character 22, state 1). There are two equally parsimonious solutions regarding the relationships of the pelodytids, in which *Tephrodytes* is more closely related to either *Miopelodytes* or *Pelodytes*. Acceptance of the former theory stipulates that character 14, sacral diapophyses widely expanded (state 1), evolves at Node C, and reverses to expanded (state 0) in *Miopelodytes*, and that four synapomorphies, all homoplasious, define the *Tephrodytes* + *Miopelodytes* clade. These characters are: sculpturing present on dermal skull bones (character 1, state 1), posterior tips of frontoparietal present (character 4, state 1), zygomatic ramus of squamosal articulates with maxilla (character 6, state 1), and vertebral neural arches elongate (character 12, state 1). All four characters also evolve at Node D, the Pelobatinae, and characters 1 and 6 further undergo reversal in *Spea*. Because the state for characters 4, 6, and 12 cannot be determined in *Miopelodytes*, one derived character, presence of dermal skull bone sculpturing, actually supports the association between *Tephrodytes* and *Miopelodytes*. On the other hand, acceptance of the hypothesis that *Tephrodytes* and *Pelodytes* are more closely related is supported by one character, sacral diapophyses widely expanded (character 14, state 1). Assuming this relationship, three characters evolve in *Tephrodytes* that also evolve in the pelobatines (Node D) and are: posterior tips of frontoparietal present (character 4, state 1), squamosal articulates with maxilla (character 6, state 1), and vertebral neural arches elongate (character 12, state 1). Furthermore, the presence of dermal skull bone sculpturing evolves at Node A, the Pelobatoidea, and reverses to absent (state 0) in *Pelodytes*. Resolution of this trichotomy probably cannot be accomplished without further knowledge of *Miopelodytes* and *Tephrodytes*.

The Pelobatidae, united at Node B by four nonhomoplasious and four homoplasious characters, contains two subfamilies: the Pelobatinae (Node D) and the Megophryinae (*Leptobranchium*). Although *Eopelobates* has recently been removed from the Pelobatoidea (Ford and Cannatella, 1993), been placed in its own subfamily, the Eopelobatinae (Špinar, 1972), and has been considered to be close to the megophryines (Zweifel, 1956; Kluge, 1966) or intermediate between the megophryines and pelobatines (Estes, 1970; Špinar, 1972), this study establishes *Eopelobates* as a member of the family Pelobatidae, and the subfamily Pelobatinae.



The Pelobatidae is a monophyletic group that shares four nonhomoplasious and four homoplasious derived characters. The nonhomoplasious synapomorphies are: postchoanal ramus of vomer absent (character 9, state 1), parahyoid bone absent (character 11, state 1), scapula long (character 15, state 1), and scapula not anteriorly overlain by clavicle (character 18, state 1). Of these, however, character 15 is the only one that is known for all members of the Pelobatidae. Other characters supporting this clade are: frontoparietal fontanelle covered by frontoparietals (character 3, state 1), which also evolves in *Tephrodytes*; medial end of coracoid expanded (character 19, state 1), which reverses to not expanded at Node C; ischium extends posteriorly (character 21, state 1), which reverses in *Pelobates* and Node C; and two free distal tarsal bones (character 23, state 1), which reverses to three free distal tarsal bones in *Eopelobates*.

Containing two clades, *Scaphiopus* and *Spea* in one, and *Eopelobates*, *Pelobates*, and *Macropelobates* in the other, the Pelobatinae (Node D) is supported by five synapomorphies, all of which exhibit some degree of homoplasy. Three of these evolve convergently in *Tephrodytes* and are: posterior tips of frontoparietals present (character 4, state 1), squamosal articulates with maxilla (character 6, state 1), and vertebral neural arches elongate (character 12, state 1). The remaining characters are: otic ramus of squamosal present (character 7, state 1), which also evolves in *Miopelodytes* and reverses to reduced in *Spea*; and spade present (character 24, state 1), which reverses to absent in *Eopelobates*.

The clade of *Scaphiopus* and *Spea* (Node E) is defined by six synapomorphies, of which half exhibit no homoplasy. These are: quadratojugal absent (character 8, state 1); postchoanal ramus of the vomer elongate (character 9, state 2); medial end of coracoid not expanded (character 19, state 0); sternum cartilaginous (character 20, state 0); ischium not extended posteriorly (character 21, state 0); and sartorius muscle and associated tendon concealed, in part, by gracilis major (character 25, state 1). Characters 19 and 21 have undergone reversal from the derived state at Node B and character 20 reverses from the derived state at Node A.

*Eopelobates*, *Pelobates*, and *Macropelobates* form a clade supported by two synapomorphies: sacral diapophyses widely expanded (character 14, state 1), which also evolves in *Tephrodytes* and *Pelodytes*; and anterior lamina of scapula present (character 16, state 0), a reversal from absent at Node A. *Pelodytes* also possesses an anterior lamina of the scapula. The association of *Macropelobates* with *Eopelobates* and *Pelobates* counters Roček's (1982) hypothesis that *Macropelobates* is closest to *Scaphiopus*. The basis of his conclusion was that *Macropelobates* shares 13 characters with *Scaphiopus* and only four with *Pelobates*. However, he was unable to determine the primitive state from the derived state for many of his characters. What Roček (1982) considered to be advanced specializations shared between *Macropelobates* and *Scaphiopus* are: lack of quadratojugal, and proportions of squamosal. A quadratojugal was not preserved with the holotype of *Macropelobates*, which has an incomplete and somewhat disarticulated skull, and Roček (1982) inferred that it was absent. However, I concluded that the presence or absence of a quadratojugal could not be determined for *Macropelobates* (see Character Analysis, character 8). This leaves the proportions of the squamosal as Roček's (1982) only synapomorphy between *Macropelobates* and *Scaphiopus*. Of the four characters shared between *Macropelobates* and *Pelobates*, Roček (1982) was unable to determine whether they were primitive or derived. In this study only two of the five synapomorphies for *Scaphiopus* and *Spea* could be determined in *Macropelobates*. These are: medial end of coracoid expanded (character 19,

state 1), and ischium expanded posteriorly (character 21, state 1). Both *Scaphiopus* and *Spea* possess the primitive state for these characters, which represents a reversal. Thus, based on the characters analyzed in this study, *Macropelobates* is more closely related to *Eopelobates* and *Pelobates* than to *Scaphiopus* and *Spea*. However, additional knowledge about *Macropelobates* may lead to a different hypothesis of relationship.

Two synapomorphies define the clade of *Eopelobates* and *Pelobates* (Node G): frontoparietal derived from three ossifications (character 2, state 1); and transverse processes of posterior presacral vertebrae oriented strongly anteriorly (character 13, state 1), which also evolves in the pelodytids. Milner (1988) was correct in his assumption that a frontoparietal derived from three ossifications was merely a synapomorphy for a clade within the Pelobatidae and not indicative of a separate origin for *Eopelobates* and *Pelobates* from other anurans as proposed by Roček (1981).

#### DISCUSSION

Examination of *Tephrodytes*, which has the diagnostic pelodytid character of a fused tibiale and fibulare, revealed there are several derived characters that also occur in some pelobatids, but not in *Pelodytes*. Thus, it seemed possible that these characters would support inclusion of the pelodytids in the Pelobatidae, and that *Pelodytes* possesses the primitive state for these characters as a result of reversal. However, the phylogeny (Fig. 9) derived from this cladistic analysis suggests that pelodytids are the sister group to the clade including the megophryines and pelobatines. Thus, it is best to retain the pelodytids in their own family. Derived characters that occur in both *Tephrodytes* and the pelobatines, including *Eopelobates*, are the result of convergence. These characters are: posterior tip of frontoparietal present (character 4), zygomatic ramus of squamosal articulates with maxilla (character 6), and presacral vertebral neural arches elongate (character 12). Furthermore, a concealed frontoparietal fontanelle evolved convergently in *Tephrodytes* and the pelobatids. Note, however, that in *Spea* the frontoparietal fontanelle is exposed, a reversal. Ford and Cannatella (1993) listed the fused tibiale and fibulare as the only unambiguous synapomorphy for the Pelodytidae. To this I add the following: anterior ramus of pterygoid elongate, and scapula with anterior tubercle.

The Pelobatidae, used here in its traditional sense to include the megophryines and pelobatines, is monophyletic. Although numerous characters support this relationship, none of them are unique to pelobatids. Three of the characters supporting the Pelobatidae that exhibited no homoplasy in this study also evolved in the Neobatrachia: parahyoid bone absent, scapula long, and scapula not overlain anteriorly by clavicle. All of the characters supporting the Pelobatinae exhibit some degree of homoplasy. This is caused, in part, by several of these features evolving convergently in *Tephrodytes*, and also by the loss of the spade in *Eopelobates*. That *Eopelobates*, used here to include *E. anthracinus* and *E. bayeri*, is a member of the Pelobatinae is well-supported, thereby making the Eopelobatinae a synonym of the Pelobatinae. One unique character, frontoparietal derived from three ossifications, supports the close relationship between *Eopelobates* and *Pelobates*. *Macropelobates* is the sister taxon to this clade, but there are no characters unique to this clade. Within this study three nonhomoplasious characters support the clade of *Scaphiopus* and *Spea*. Of these only one, sartorius muscle and associated tendon partially concealed by gracilis major, appears to be unique. The

elongate postchoanal ramus of the vomer also occurs in the rhinophrynid, *Chelomophrynus*, and the quadratojugal has also been lost in *Ascaphus*, *Leiopelma*, and *Notobatrachus*.

In conclusion, a phylogeny for the Pelobatoidea is provided. This phylogeny follows the more traditional approach in that the pelobatids and pelodytids are sister clades and the megophryines are included in the Pelobatidae. Relationships within the Pelodytidae are unresolved, and more information on the extinct members is required. Within the Pelobatidae, the relationships of *Eopelobates* and *Macropelobates* as presented here differ from previous phylogenetic hypotheses. However, additional knowledge of these taxa could result in a different phylogeny.

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